Regeneration microsites of *Picea abies* seedlings in a windthrow area of a boreal old-growth forest in southern Finland

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Microsite characteristics of established *Picea abies* seedlings were studied in a windthrow area of a *Picea*-dominated old-growth forest in the southern boreal zone of Finland. The seedling (height 3–30 cm) density, most of which was *Picea* (87%, ca. 31 000 ha^{-1}), was high (ca. 36 000 ha^{-1}). Seedlings of *Betula pubescens* (ca. 2000 ha^{-1}) and *Sorbus aucuparia* (ca. 2100 ha^{-1}) were also abundant. The distribution of *Picea* seedlings across microsite types was significantly nonrandom. *Picea* seedlings were found in microsites created by windthrow disturbance, particularly advanced-decay wood, and uprooting pits and mounds. Sixty-three percent of the *Picea* seedlings occurred in these microsites, although they only covered ca. 28% of the study area. As a result of this pattern, *Picea* seedlings were aggregated in space and the majority of seedlings grew on microsites located above average local ground level. These results demonstrate the importance of disturbed microsites for the natural regeneration of *Picea* after windthrow disturbance. In managed forests, when naturally regenerating *Picea* on fertile sites, effort should be taken to create regeneration microsites similar to those created by natural disturbances, i.e. uprooting niches and decaying logs. These microsites are also important for the maintenance of biodiversity in managed forests.

Key words: competition, disturbance, gap regeneration, heterogeneity, Norway spruce, regeneration niche

Introduction

Studies on natural regeneration of Fennoscandian boreal forests have traditionally focused on successions following severe fire disturbance (Aaltonen 1919, Sarvas 1938, Sirén 1955, Yli-Vakkuri 1961, Zackrisson 1977). However, natural forests experience a wide range of disturbance factors that can create growing space and facilitate forest regeneration (Engelmark & Hytteborn 1999). These disturbance factors include windthrows, low-severity ground fires, snow loads, pathogens, and insects (Kuuluvainen 1994). Already in the 1930s, Sernander (1936) emphasized the importance of storm gaps in the regeneration dynamics of *Picea* forests in
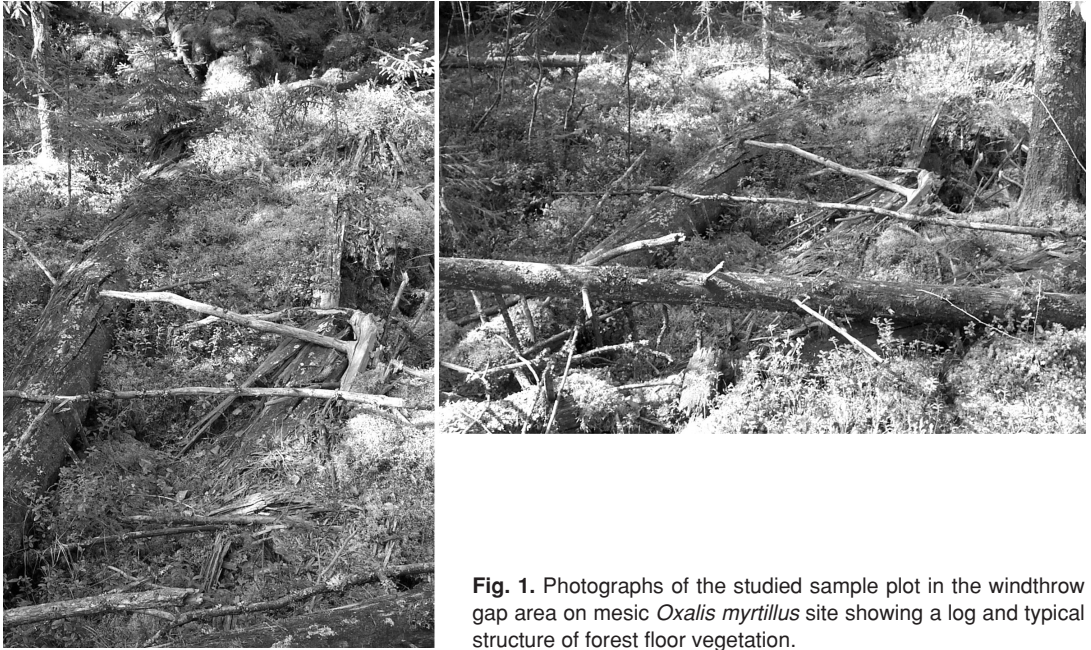
Fig. 1. Photographs of the studied sample plot in the windthrow gap area on mesic *Oxalis myrtillus* site showing a log and typical structure of forest floor vegetation.

Sweden. During recent years numerous studies have demonstrated the important role of different kinds of disturbances in the regeneration dynamics of boreal forests (Hytteborn *et al.* 1987, Leemans 1991, Hofgaard 1993a, 1993b, Liu 1993, Kuuluvainen 1994, Hörnberg *et al.* 1997, Kuuluvainen & Juntunen 1998, Kuuluvainen & Rouvinen 2001).

Even small-scale disturbances can create regeneration microsites for seed germination and seedling growth (Yli-Vakkuri 1961, Kuuluvainen 1994). In particular, decomposed logs and uprooting microsites (pits and mounds) provide favorable microsites for regeneration of trees (Sirén 1955, Hofgaard 1993a, Hörnberg *et al.* 1997). In Fennoscandian conditions, the significance of such microsites for seedling establishment is often considered to be smaller in dry *Pinus sylvestris*-dominated forests with a thin humus layer as compared with moist *Picea abies*-dominated forests with abundant understory vegetation and a thick humus layer (Kuuluvainen 1994).

Beyond the direct influences, disturbances also indirectly affect seedling establishment and growth through changes in the composition of understory vegetation caused by changes in local microclimate (e.g. Hertz 1932, Peterson &

Pickett 1995). Thus, a windthrow gap is usually very heterogeneous with fine-scale variation in topography, substrate quality, resource availability, and vegetation structure (Hertz 1932, Kuuluvainen & Juntunen 1998). This internal fine-scale heterogeneity is superimposed by larger scale within-gap gradients in microclimate and competitive interference by the dominant trees surrounding the gap (Aaltonen 1919, Kuuluvainen & Pukkala 1989, Kuuluvainen *et al.* 1993). Thus, a gap usually possesses an extensive range of different microsites. However, it is not well understood how the accessibility of different microsites contributes to the regeneration process. Important factors related to the suitability of regeneration microsites include abiotic factors, the occurrence of predators, competition, and possible chemical interactions (Yli-Vakkuri 1961, Zackrisson & Nilsson 1992). Regeneration is also affected by the highly variable seed production in northern forests (Koski & Tallqvist 1974).

Forest management methods aimed at more natural and ecologically sustainable forestry are currently being developed using natural disturbances and stand structures as a model (Angelstam 1996, Hunter 1999, Harvey *et al.* 2002, Kuuluvainen 2002). These "gap-based" silvi-

cultural methods often include the use of small and/or irregularly shaped clear cuts, fragmented with islands of retention trees (Coates & Burton 1997). For developing such silvicultural methods, a better understanding of tree regeneration ecology in gap environments is needed (Coates & Burton 1997). For example, in managed forests on fertile sites, the natural regeneration of *Picea* forests, e.g. using a shelterwood method, has proved to be problematic under Fennoscandian conditions (Leinonen *et al.* 1989). Perhaps new insights for developing regeneration methods can be obtained from a deeper understanding of the regeneration dynamics after natural disturbances.

The aim of this study was to examine the availability and importance of different microsite types and the effect of competing trees and other vegetation on the establishment of *Picea* seedlings in a windthrow area of a boreal old-growth forest. We specifically wanted to elucidate the properties of regeneration microsites of *Picea* seedlings and how they differ from the overall availability of microsites in the windthrow area.

Materials and methods

Study area

The study site is located in the Nuijakorpi forest protection area of southern Finland, close to the Hyytiälä forestry field station of the University of Helsinki (61°50´N, 24°17´E, alt. 150 m a.s.l.). The area belongs to the southern boreal vegetation zone (Ahti *et al.* 1968). The effective temperature sum (5 °C threshold) is approximately 1150 d.d., and the annual mean temperature is +3.5 °C. Mean annual precipitation is 700 mm, 250 mm of which manifests as snowfall (Anon. 1994).

In the 1950s, a windthrow disturbance area of several hectares was formed in the old-growth *Picea abies* forest. Based on the study area having fallen wood of different decay classes, the forest structure has likely been modified by several subsequent windthrow events, affecting a vast number of trees and enlarging the windthrow area. Thus, the windthrow area consists of a mosaic of smaller areas of different disturbance severity and time.

The site selected for this study has lost most of its overstory trees, i.e. the disturbance can be regarded as stand-replacing. The site is located in the northern part of a larger windthrow area. A plot of 50 m × 60 m (0.3 ha) was marked in the field so that the longer side was in the north–south direction. Around the plot, a 10-m-wide buffer zone was delineated, and competing seedlings and large trees in the zone were mapped and measured.

The study site is classified as a fertile *Oxalis–Myrtillys* type according to the Finnish site classification system (Cajander 1909). *Picea* dominated the surrounding forest, as well as the site, before canopy destruction. In addition, individuals of *Betula pendula*, *B. pubescens*, *Pinus sylvestris*, *Populus tremula*, *Sorbus aucuparia*, *Alnus incana*, *A. glutinosa*, *Salix caprea*, and other *Salix* species were present. The dominant trees were 100–150 years old. The field- and bottom-layer vegetation mainly comprised dwarf shrubs (*Vaccinium myrtillus* and *V. vitis-idaea)* and mosses (*Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum* spp.) (Fig. 1).

Sampling and measurements

The main objective was to compare the properties of the microsites of established *Picea* seedlings with microsites lacking seedlings. For this purpose, 150 random points were located in the study plot with the help of a 10 m × 10 m grid. These random points were the centers of the sample plots without seedlings. The stem base of the *Picea* seedling closest to each random point formed the center of a seedling plot. Both random and seedling plots were circular with an 8-cm radius (area 200 cm²).

Seedlings that were taller than 3 cm but shorter than 30 cm were selected. These criteria were chosen because the sampled seedlings had already passed the early developmental phases, often associated with high mortality, but were still growing within a clearly distinguishable microsite. The sample contained 150 random plots and 150 *Picea* seedling plots.

Estimation of microsite areas

A 1 m × 1 m quadrate was placed around each random point ($n = 150$) to estimate the horizontally projected areas of different microsite types occurring in the study area. Cover percentages of microsite types were visually estimated in each quadrate. We identified eight different microsites; habitats 1–3 represent "undisturbed" habitats, while habitats 4–7 were formed by disturbance (Table 1). The decay stage of logs and stumps was defined using a five-stage classification according to Renvall (1995), based on the softness of the wood and the occurrence of epiphytes on logs (Table 2).

Microsite descriptions and measurements

Differences between microsite characteristics of random points/plots and seedling points/plots were based on the following measurements and descriptions: (1) microsite type, (2) relation to the horizontal projection of crown projection of dominant trees (inside/outside crown projection), (3) ground vegetation type and cover, (4) relative radiation level, and (5) competitive interference from surrounding seedlings and large trees, as described by calculated competition index values.

Nine microsite types defined the location of random and seedling points in the microsite

Table 1. Microsite types used in estimating the cover percentages of different microsites.

Microsite class	Definition
1. Level ground	Vegetation-covered soil with "normal topography", i.e. height differences < 10 cm within the quadrate
2. Hump	Clearly elevated, height > 5 cm compared with the surrounding level ground
3. Depression	Clearly lower, depth > 5 cm compared with the surrounding level ground
4. Fallen log	Log laying on the ground, varying decay stages
5. Stump	Stumps of broken trees, varying decay stages
6. Uprooting pit	Formed in the gap-creating windthrow
7. Uprooting mound	Formed in the gap-creating windthrow
8. Other	Stone, living tree, etc.

Table 2. Decay stage classification used (Renvall 1995).

Decay stage	Properties of log
1	Recently fallen tree, wood hard, often with bark; knife penetrates only a few mm; epiphytes are those occurring on standing trees
2	Wood hard, often with bark; knife penetrates a few cm; some epiphytes
3	Wood fairly soft, with some bark already removed; knife penetrates several cm quite easily; epiphytic lichens and mosses may be abundant in places
4	Wood soft, often without bark, and covered with epiphytes; knife penetrates easily all the way through; epiphytic mosses and lichens as well as vascular plants abundant
5	Wood very soft, often totally covered with epiphytes; knife penetrates easily all the way through; epiphytes are largely those also growing on the ground, lichens and dwarf shrubs; log is barely distinguishable from the surrounding level ground

mosaic: (1) on level ground, (2) on a hump, (3) in a depression, (4) on a log, (5) beside a log, (6) in an uprooting pit, (7) on an uprooting mound, (8) on a stump, and (9) beside a stump. These types differed slightly from those used in areal estimates (*see* Table 1) because it was deemed necessary to separate "on decomposed wood" and "beside decomposed wood" into different regeneration microsites.

Vegetation cover analysis of ground and bottom layers was carried out for both random and seedling plots. Area not covered by vegetation was divided into (1) bare ground, (2) litter, (3) dead and living woody material, and (4) stone.

Competitive interference from the adjacent woody vegetation was described with competition indices based on the size and location of adjacent seedlings (seedling competition index) and large trees (tree competition index). We measured the height, distance, and direction of the three closest seedlings (height < 2 m) located within a 2-m radius of the sample seedling, and the species, diameter at breast height (DBH), distance, and direction of the three closest dominant trees.

The seedling competition index for each sample seedling was computed as the weighted sum of vertical angles from the seedling apex to the crown tops of the surrounding seedlings. Angle sums were multiplied by a weighting factor according to compass direction to account for the asymmetry of the shading effect. Competitors in the four main compass directions had the following weighting factors: north 0.5, south 1.5, east 1.0, and west 1.0; directions between these were assigned intermediate weights (Pukkala & Kolström 1987).

The seedling and tree competition indices for seedling *j* were calculated using the equation:

$$\mathrm{CI}_j = \sum_{i=1}^{n} c\beta_i, \; h_i > h_j \qquad (1)$$

where CI is the competition index, *i* the competing seedlings/trees, *n* the number of competing seedlings, and *c* the direction-weighting factor. When calculating the seedling competition index, β was the vertical angle between the seedling apex and the top of the adjacent seedling, and *h* the seedling height. The tree competition

index describing the competition of adjacent large trees was computed in the same manner, but instead of the vertical angle, the horizontal angle from seedling to the perpendicular diameter at breast height was used.

To describe relative differences in the radiation environment between sampling points, we measured the photosynthetically active radiation, PAR (μE m^{-2} s^{-1}), with a Licor radiation sensor. The measurements were carried out on an ordinary overcast day. The random points were measured at a height of 30 cm above ground, and seedling points just above each seedling apex. To account for the variation in above-canopy radiation levels during the measurement period, the time of each measurement was recorded and a reference measurement was taken every 15 minutes at a fixed point in the middle of the study area.

The measurements were then adjusted by removing the time-dependent variation in above-canopy radiation levels, as described by the reference measurements, from the initial measurements. This was accomplished by dividing the measurement at each random or seedling point by the closest reference measurement in time taken at the midpoint of the study plot.

Sample seedling measurements

The following variables were determined for each sampled seedling: (1) height (cm), (2) height growth, i.e. length of the leader shoot (mm), (3) vigor class (1 = healthy, 2 = weakened, 3 = suffering, 4 = dying, 5 = dead), (4) damages (1 = broken top, 2 = other mechanical damage, 3 = fungi or insect damage, 4 = declined vigor due to shading), and (5) local elevation in microtopography in ±5 cm classes from the surrounding average ground level.

Statistical analyses

Statistical testing of differences between microsite characteristics of the random and seedling plots was carried out as comparisons between two populations. Random and seedling plots were considered as independent samples.

Because the requirements of parametric tests could not be met, we used the Kolmogorov-Smirnov test (K-S test) for continuous variables. This test takes into account differences both in the shape and location of distributions.

The microsite distributions in random versus seedling plots were compared using a log-likelihood test value:

$$G^2 = 2\sum_{i=1}^{k} o_i \ln \frac{o_i}{e_i} \qquad (2)$$

where k is the number of microsite classes, and o_i is the observed and e_i the expected frequency in class i. Microsite proportions based on random plots were used as expected frequencies which were tested against observed microsite distributions of seedling plots.

Results

Occurrence of microsite types

The dominant habitat type on the plot was undisturbed level ground, covering 47.2% of the 0.3-ha study area. The undisturbed habitats not created or affected by windthrow disturbance, i.e. level ground, small humps, depressions, and others, accounted for 69.3% of the plot area. Logs covered 19.5% of the area, and uprooting pits and mounds 5.1% and 2.9%, respectively; thus, together these disturbed habitats covered 27.5% of the study plot area (Table 3).

Fallen woody material, i.e. logs and stumps, covered 22.7% of the studied site. The area covered by fallen wood of different decay classes was as follows: stage 1: 0.5%, stage 2: 3.7%, stage 3: 5.7%, stage 4: 4.8%, and stage 5: 4.8%. Thus, logs represented different decay stages, except for decay stage 1, quite evenly.

Density and spatial distribution of seedlings

Taking into account all tree species, the density of seedlings (height 3–30 cm) was ca. 33 800 ha^{-1}. *Picea* was most abundant (31 133 ha^{-1}, 87%), followed by *Sorbus aucuparia* (2067 ha^{-1}, 5.8%) and *Betula pubescens* (2000 ha^{-1}, 5.6%). *Salix* spp. (333 ha^{-1}, 0.9%), *Betula pendula* (133 ha^{-1}, 0.4%), and *Pinus sylvestris* (133 ha^{-1}, 0.4%) were less frequent, together comprising ca. 600 seedlings ha^{-1} (ca. 2% of seedlings).

The density of seedlings varied greatly in the randomly positioned quadrats. The number of quadrats in different seedling density classes were: 0 seedlings — 59 quadrats, 1–10 seedlings — 80 quadrats, 11–20 seelings — 8 quadrats, 21–30 seedlings — 0 quadrats, 31–40 seedlings — 2 quadrats, 41–100 seedlings — 0 quadrats, and 100–110 seedlings — 1 quadrat.

Sample seedlings

The height distribution of the sampled *Picea* seedlings was rather even, but small seedlings (height 3–5 cm) were most abundant (Fig. 2). The tallest seedlings had apparently been established before the windthrow disturbance. Most of the seedlings (80.7%) were classified as healthy. Of the remainder, 12% were classified as weakened, 4.7% as suffering, and 2.6% as dying.

Occurrence of seedlings in microsites

Seedlings clearly occurred more often in disturbed microsites than could be expected from their share of the land area (Table 4). Accordingly, the distribution of *Picea* seedlings into microsite types was significantly different from that of random points ($p < 0.001$, log-likelihood test).

Because level ground was the predominant microsite, the majority of random points also

Table 3. Estimated proportions of the cover percentages of different microsites.

Microsite type	Percentage of ground area
Level ground	47.2
Humps	11.6
Depressions	9.6
Logs	19.5
Stumps	3.2
Uprooting mounds	5.1
Uprooting pits	2.9
Other (stone, tree)	0.9

occurred in this habitat. In contrast, *Picea* seedlings had established themselves most often on or immediately beside decayed wood (57%). However, level ground also had a considerable proportion (21%) of seedlings. Of all *Picea* seedlings, 13% occurred in pits or on mounds, i.e. microsites of disturbed soil. Overall, the proportion of seedlings on or beside decayed wood or in uprooting niches (ca. 70%) was much higher than their share of ground area (ca. 28%), while on level ground the situation was the reverse.

Random points on fallen wood were distributed rather evenly among different decay stages, except for decay class 1. *Picea* seedlings, by contrast, occurred most often on logs in more advanced decay stages (stages 4 and 5) (Table 5).
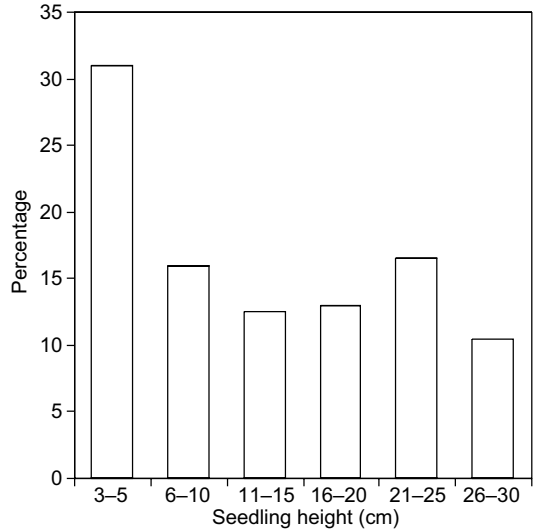
Vertical arrangement of seedlings in the microtopography

The elevation of *Picea* seedlings (location of stem base) in the local microtopography relief was measured in relation to the surrounding average ground level. Accordingly, seedlings in uprooting pits, for instance, had negative values, while ones on mounds or logs had positive values (Fig. 3).

Most of the *Picea* seedlings grew above local ground level, and in this group, seedlings that grew ca. 10–15 cm above ground level were most plentiful (Fig. 3). However, level ground (0-class) was the microtopography height class with the largest number of seedlings. Only a small proportion of seedlings grew lower than average ground level.

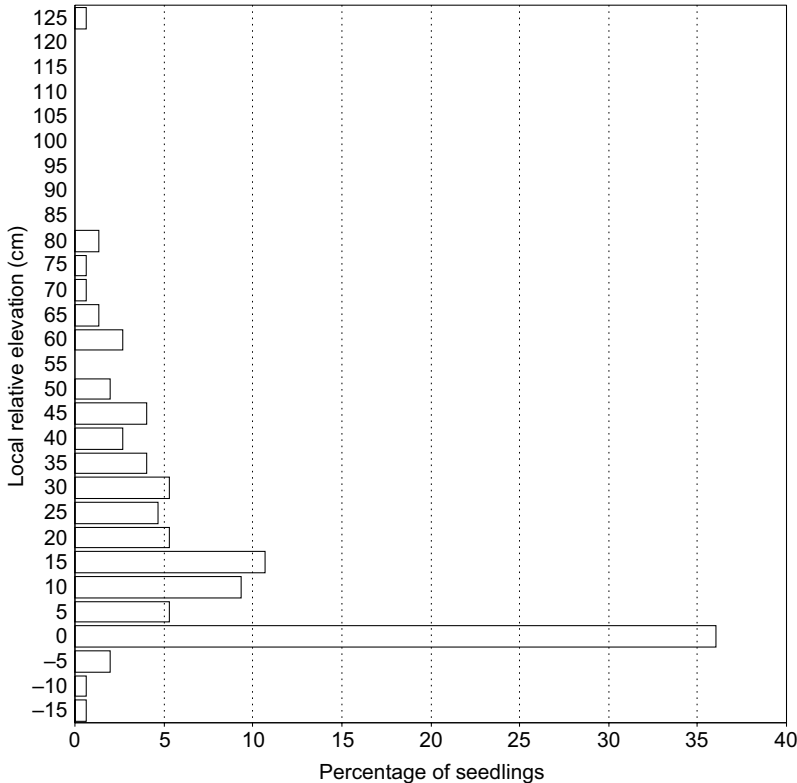**Fig. 2.** Height distribution of *Picea* seedlings (*n* = 150).

Understory vegetation

Vegetation in the study plot was characterized by 41 species or species groups. Cover percentages and occurrence frequencies are shown in Table 6. The mean vegetation cover of ground vegetation was 57.6% in the random plots and 61.6% in the *Picea* seedling plots.

Both in random and seedling plots, the ground vegetation was dominated by dwarf shrubs *Vaccinium vitis-idaea* and *V. myrtillus* while *Pleurozium schreberi* and *Dicranum* sp. dominated the bottom layer. The predominant species were the same in both random and seedling plots, and no

Table 4. Percentage distribution of random points and *Picea* seedlings in different microsite types.

Microsite type	Random points	*Picea* seedlings
Level ground	32.0	20.7
Humps	24.6	8.0
Depressions	8.0	1.3
On decayed wood	17.4	31.4
Beside decayed wood	12.0	25.3
Uprooting mounds	2.7	6.0
Uprooting pits	3.3	7.3

Table 5. Percentage distribution of random points and *Picea* seedlings on and beside coarse woody debris of different decay classes.

Habitat	Decay class	Random points	*Picea* seedlings
On logs or stumps	1	0.0	0.7
	2	4.0	4.0
	3	6.0	6.7
	4	4.0	8.7
	5	3.4	11.3
Beside logs or stumps	1	0.0	0.0
	2	2.0	3.4
	3	5.3	5.3
	4	2.7	5.3
	5	2.0	11.3

Fig. 3. Vertical distribution of *Picea* seedlings in the local microtopography relief of the windthrow area.

significant differences were present between any of the recorded species or species groups, except for the obvious higher coverage of *Picea* in seedling plots than in random plots. However, there was a weakly significant difference in *Dicranum* sp., this species group being more abundant in seedling than in random plots (Table 6).

Competitive environment of seedlings

Picea seedlings were more often situated outside horizontal tree crown projections than random points. Of the random points, ca. 75% (*n* = 113) were located under tree crowns, while the corresponding proportion in *Picea* seedlings was ca. 65% (*n* = 98).

The tree competition index values (Eq. 1), describing the competitive effect of large trees, were generally higher for seedlings growing in undisturbed microsites (habitats 1–3) as compared with disturbed microsites (habitats 4–9). However, this difference was not statistically significant (K-S test).

The seedling competition index, describing the competitive effect of adjacent seedlings, was significantly higher for seedlings growing in disturbed microsites as compared with seedlings growing in undisturbed microsites (K-S test: *p* = 0.01). This difference apparently results from the clustering of *Picea* seedlings on microsites created by the disturbance event.

No significant differences existed between the radiation environments of *Picea* seedlings and those of the random points (Table 7). In both random points and seedlings under crown projections, the radiation levels were significantly lower than those outside crown projections; *p* values of the Kolmogorov-Smirnov test for random and *Picea* points were 0.001 and < 0.001, respectively. The highest average radiation levels were recorded on uprooting mounds.

Discussion

The variety of microsites created by the windthrow disturbance was important for *Picea*

Table 6. Species cover (%) and frequency (%) in field- and bottom-layer vegetation in random and seedling plots; *p* values show the Kolmogorov-Smirnov test results of similarity between distributions among the two samples; only significant *p* values are reported.

	Random plots		Seedling plots		*p* Random/Seedling
	Cover	Frequency	Cover	Frequency	
Field-layer species					
Picea abies	0.2	6.67	14.0	100.00	0.000
Betula pubescens	0.1	0.67	0.1	2.00	–
Betula pendula	0.0	0.00	0.1	1.33	–
Salix sp.	0.1	0.67	0.1	0.67	–
Vaccinium myrtillus	7.4	50.67	6.7	46.67	–
Vaccinium vitis-idaea	8.8	61.33	9.0	60.67	–
Empetrum nigrum	0.1	0.67	0.1	1.33	–
Rubus chamaemorus	0.3	4.00	0.1	2.67	–
Rubus idaeus	0.1	0.67	0.0	0.00	–
Dryopteris carthusiana	1.1	6.00	0.3	2.67	–
Equisetum sylvaticum	0.6	3.33	0.3	4.67	–
Lycopodium annotinum	0.1	0.67	0.3	1.33	–
Epilobium angustifolium	0.0	0.00	0.3	0.67	–
Gymnocarpium dryopteris	0.1	0.67	0.2	2.00	–
Linnea borealis	0.2	6.00	0.3	6.67	–
Deschampsia flexuosa	0.0	0.00	0.1	1.33	–
Calamagrostis arundinacea	0.1	0.67	0.0	0.00	–
Trientalis europea	0.2	4.67	0.2	5.33	–
Oxalis acetosella	0.5	10.67	0.4	8.67	–
Maianthemum bifolium	0.1	2.00	0.1	0.67	–
Carex sp.	0.6	17.33	0.8	22.67	–
Pyrola sp.	0.4	2.67	0.1	0.67	–
Festuca ovina	0.1	3.33	0.1	3.33	–
Total	20.7		33.4		
Bottom-layer species					
Pleurozium schreberi	19.5	65.33	22.0	72.67	–
Hylocomium splendens	6.1	31.33	6.3	35.33	–
Brachythecium spp.	2.7	24.00	1.5	12.00	–
Ptilium crista-castrensis	0.3	1.33	0.1	0.67	–
Ptilidium pulcherrimum	1.2	10.67	0.5	8.00	–
Pohlia nutans	1.3	11.33	1.8	11.33	–
Dicranum spp.	13.3	64.67	16.0	74.00	0.059
Polytrichum spp.	1.5	12.67	2.4	18.00	–
Ceratodon purpureus	0.1	1.33	0.9	2.00	–
Sphagnum sp.	9.7	25.33	8.5	22.67	–
Cladonia arbuscula	0.2	2.67	0.1	1.33	–
Cladonia rangiferina	0.1	2.00	0.1	0.67	–
Cladonia cornuta	0.8	11.33	0.7	9.33	–
Cladonia coccifera	0.0	0.00	0.1	0.67	–
Cladonia spp.	0.3	10.00	0.7	13.33	–
Cetraria sp.	0.2	2.67	0.1	2.00	–
Parmeliopsis ambigua	0.1	2.00	0.1	0.67	–
Parmelia sp.	0.3	2.00	0.3	7.33	–
Total	57.6		61.6		
Litter	36.6	99.33	33.5	99.33	–
Fallen wood	4.6	16.67	2.7	12.67	–
Living tree	0.1	2.67	0.1	2.67	–
Bare ground	1.1	2.00	1.3	3.33	–
Stump	0.0	0.00	0.6	3.33	–
Stone	0.1	0.67	0.2	1.33	–
Total	100		100		

regeneration on this fertile *Oxalis–Myrtillus* site. This was shown by *Picea* seedlings occurring significantly more often than would be expected on disturbed microsites, i.e. on and beside decayed wood and uprooting niches. Decayed wood and uprooting pits and mounds hosted 63% of sampled *Picea* seedlings, although these microsite types covered only 28% of the land area studied. In contrast, undisturbed microsites, i.e. level ground, humps, and depressions, covered ca. 70% of the area but contained only 30% of the seedlings. Thus, *Picea* was efficiently able to utilize both decayed woody debris and their surroundings (logs, stumps) as "safe regeneration sites" (Harper *et al.* 1965). Overall, gaps in the ground- and bottom-layer vegetation and the exposed mineral soil formed by treefalls had a strong positive effect on *Picea* seedling establishment (also Nakashizuka 1989).

These results are in agreement with earlier studies. For example, Hytteborn *et al.* (1987), Hofgaard (1993a), and Hörnberg (1995) have demonstrated the importance of sufficiently decayed wood for the regeneration of moist spruce forests in northern Fennoscandia. Establishment of seedlings on decayed logs is due to advantageous moisture and light conditions, while competition of other plants is restricted. In addition, decayed wood can be rich in nutrients as a result of microbial nitrogen fixation (Jurgensen *et al.* 1987, Hendrikson 1991). However, it is noteworthy that logs must be in an advanced stage of decay for regeneration to occur. According to Holeksa (1998), larger logs are more favorable for regeneration than smaller logs. This relationship was not, however, examined in this study.

Also the benefit of microsites with exposed mineral soil for tree regeneration has been dem-

onstrated. In Finland, Yli-Vakkuri (1961) found that seed germination and seedling survival are higher on mineral soil than on undisturbed soil. Kuuluvainen and Juntunen (1998) reported that in a windthrow gap in a *Pinus sylvestris*-dominated forest both *Pinus* and *Betula* seedlings were strongly aggregated in disturbed microsites, especially uprooting pits and mounds. Skoglund and Verwijst (1989) documented the frequent establishment of birch on tilted root plates and logs in storm gaps along river shores in eastern central Sweden. Aaltonen (1919) demonstrated that in the dry *Pinus* forests of northern Finland seedlings were most plentiful along decomposed fallen trunks and in uprooting niches.

The microtopography of sites disturbed by treefalls differs considerably from that of undisturbed locations (Beatty & Stone 1986, Peterson & Pickett 1990, Peterson *et al.* 1990). Concentrations of fallen wood and uprooting niches are characterized by steep fine-scale topographic gradients. In the windthrow gap area, *Picea* seedlings were most often located above average local ground level. It is probable that in the studied mesic *Oxalis–Myrtillus* site type, competition due to abundant vegetation at level ground is rather intense, and thus, an elevated position significantly contributes to survival and successful establishment of seedlings (Hertz 1932, Jäderlund 2001). This was demonstrated by the relatively low density of seedlings in locations with undisturbed field- and bottom-layer vegetation.

The comparison of random plots and sample seedling plots revealed no significant differences in vegetation characteristics, with the exception of one group of mosses (*Dicranum* sp.), where the difference was weakly significant. This result may be due to the relatively long time elapsed since the windthrow disturbance, which has facilitated an overall recovery of the plant community. As random points were most often located on undisturbed soil, and this habitat type hosted a fair number of seedlings, the sampled seedlings may also have established more often on undisturbed ground than would be expected based on their share of the seedling population.

Kuuluvainen and Juntunen (1998) used the same sampling method to examine regeneration microsites of *Pinus* and *Betula* in a more recent

Table 7. Relative radiation levels ($\mu E\ m^{-2}\ s^{-1}$) of *Picea* seedlings and random points.

Radiation level	*Picea* seedlings	Random points
Mean	0.43	0.42
Minimum	0.05	0.02
Maximum	1.19	1.21
Variance	0.06	0.08
Coefficient of variation	0.55	0.67

windthrow gap in a *Pinus*-dominated forest on the dryish *Vaccinium* site type in the middle boreal zone of Finland. They found that seedlings of these two tree species were even more strongly confined to disturbed microsites (82% of *Pinus* and 98% of *Betula* seedlings) than the *Picea* seedlings in our study (63%). This result was somewhat contrary to expectations, as in drier site types seedling establishment has been often considered to be less restricted to specific microsites as compared with more mesic site types (Kuuluvainen 1994). Apparently, the mechanisms involved are more complicated than previously thought, and time since the disturbance event may play an important role as these two studies represent different times from windthrow disturbances. This may also explain why Kuuluvainen and Juntunen (1998) found significant differences for some plant species or species groups between random plots and plots of *Pinus* and *Betula*. However, for most species or species groups, no significant differences were detected (Kuuluvainen & Juntunen 1998; Table 5).

The aggregation of seedlings on disturbed microsites may result in higher interseedling competition than between seedlings growing on undisturbed microsites, as indicated by the computed seedling competition indices. On the other hand, more resources may be available on disturbed microsites as compared with undisturbed ones, which would lower competitive interseedling interference, at least for soil resources.

Seedlings were found less often under tree crowns (ca. 65%) than random points (75%), but this difference was not significant. However, from these relatively high percentages, it can be concluded that despite the windthrow a significant number of smaller understory trees survived the disturbance event and grew tall enough to shade smaller seedlings in the area. Accordingly, the crown coverage was quite high when viewed from the perspective of small seedlings.

Conclusions

Our results demonstrate that the windthrow disturbance created disturbed microsites and small-scale variation in microtopography, which are important for the tree regeneration process. In managed forests, these disturbed regeneration microsites are not formed, as uprootings do not occur and logs or large-sized trees are not left in the forest. This leads to a lack of suitable natural regeneration microsites for *Picea* and may be an important reason for the difficulties commonly faced in the natural regeneration of *Picea* forests in fertile managed stands in southern Finland (Leinonen *et al*. 1989). Thus, when naturally regenerating *Picea* on fertile sites, effort should be invested in creating similar microsites to those created by natural disturbances, i.e. uprooting niches and decayed logs. As these microsites are also important for the maintenance of overall species diversity in the forest, this would further contribute to ecological sustainability of forest management.

Acknowledgments

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